and a clear fluid passes through. This gives no coagulum on dilution, but the corpuscles, if removed from the filter and suspended in a saturated solution of sulphate of magnesia, exude abundance of the coagulable material on the addition of water. This is not unlike the results obtained by Mr. Wooldridge in the Leipzig Laboratory with white corpuscles from the lymphatic glands and from the blood of mammals.*

I have spoken throughout of the substance, upon the formation or exudation of which from the corpuscles the clotting of the Echinus fluid seems to depend, as coagulable material, and not as fibrine. It does not, in fact, either in its chemical reactions or in its microscopic characters, bear any sort of resemblance to the fibrine of vertebrate blood, but appears to be more nearly allied to mucin, although the possession by it of the remarkable property of spontaneously shrinking after its first formation gives it a deceptive similarity to fibrine.

The detailed account of the above investigation will be published in the "Journal of Physiology."†

III. "Preliminary Note on the Structure, Development, and Affinities of Phoronis." By W. H. CALDWELL, B.A., Caius College, Cambridge, Demonstrator of Zoology. Communicated by Dr. M. FOSTER, Sec. R.S. Received November 24, 1882.

Owing to the time that must necessarily elapse during the preparation of plates, it has seemed to me advisable to publish the following preliminary account of my observations on the anatomy and development of Phoronis. These studies were made for the most part in the Zoological Station at Naples. I am much indebted to Dr. Anton Dohrn for his great kindness and assistance. I have not thought it necessary in this preliminary note to refer at any length to the observations of previous investigators,‡ and the bearing of the facts on recent morphological speculation has at most been indicated in the briefest possible manner. I would, however, specially refer to some observations on the development made in the summer of 1881, by Dr. Hatschek, who most generously not only sent me material, but on his return to Naples resigned his work and drawings to me.

* "Proc. Roy. Soc.," vol. 32, p. 413 ; and "Archiv. f. (Anat. u.) Physiol.," 1881.

† The opportunity for carrying on these observations was afforded me at the Scottish Zoological Station of Professor J. Cossar Ewart and Mr. G. J. Romanes.

‡ J. Müller, Wagener, Krohn, Gegenbaur, Schneider, Kowalewsky, Metschnikow, Claparède, Wright, Dyster, Van Beneden, McIntosh, Wilson, &c.

Unfortunately, I have been unable to confirm Dr. Hatschek's account in several points. To do justice to this, I reserve a fuller account of the controverted points for my complete paper, when I hope also to reproduce Dr. Hatschek's figures of the living larvæ.*

Structure of Adult Phoronis.

The mouth and anus are situated at one end. The short line between them is the median dorsal line. Between mouth and anus lies an epistome. *This epistome is the persistent præoral lobe* of the larva. New tentacles of the lophophore round the mouth are added on either side of the median dorsal line. There is a mesoblastic skeleton in the lophophore. The ventral surface is produced into a "foot," which constitutes the main part of the animal.

This determination of the surfaces depends on the development to be described below.

Epithelium of the Body.

Nervous processes of the ectoderm cells retain their connexion with the ectoderm, and concentrations, both of fibres and ganglion cells, occur in the skin outside the homogeneous basement membrane. The central nervous system remains therefore in the epidermis, *representing* the primitive condition.

Concentrations of the nervous system take place round the mouth to form a *postoral nerve-ring*. The anus lies outside this. The ring follows the line along the base of the tentacles, and has therefore like them the form of a horse-shoe. In front of this ring are situated a pair of sense organs, which I shall speak of as "ciliated pits." They lie in the concavity of the lophophore, on either side of the anus. They have the characteristic structure of sensory epithelium, consisting of sense cell, ganglion, and nerve-fibres. Sars† has figured in Rhabdopleura a pair of ciliated protuberances in what I hope to show is an homologous position.

A further concentration takes place in the form of a cord, which runs from the median dorsal part of the nerve-ring two-thirds of the length of the foot along its left side. It is therefore asymmetrical, and lies in the epidermis outside the basement membrane. Inside this nerve-cord lies an apparently hollow tube. This tube recalls the so-called large fibres of Chætopoda.

The alimentary canal is in the form of a ciliated tube, which may

* It is not to be understood that Dr. Hatschek agrees with my account of the facts of development.

† G. O. Sars, "On Rhabdopleura mirabilis," "Q. J. M. S.," vol. xiv, new series.

be divided into four main divisions, each characterised by a special epithelium :—

1. Œsophagus.
2. 1st stomach.
3. 2nd stomach.
4. Intestine.

The transition from the second to the third of these divisions is very marked. The third forms a small strongly ciliated chamber where the gut doubles on itself at the end of the foot.

The Body-Cavity

is lined throughout by peritoneum, which passes into mesenteries, dividing the cavity into several chambers. There is a ventral mesentery extending the whole length of the foot, attaching the outside of both descending and ascending limbs of the alimentary canal to the body-wall. Besides this there are two lateral mesenteries, which pass from the sides of the stomach to the body-wall. By these three mesenteries the *body-cavity is divided into three chambers*, viz., two anterior and one posterior. The lateral mesenteries end freely before the blind end of the foot is reached, so that all the chambers are here in full communication.

An important secondary connexion takes place some little way below the tentacles. The intestine attaches itself to the left lateral mesentery, dividing it into two parts, a shorter, attaching the intestine to the stomach, and a longer, attaching the intestine to the body-wall. Throughout the greater part of the foot this results in the posterior of the three chambers being divided into two.

The body-cavity is further divided by a septum, which passes from the line of the nerve-ring in the body-wall to the œsophagus, into two regions, viz. :—(i,) the space in front of the septum, *i.e.*, the body-cavity in the epistome and the tentacles ; (ii,) the space behind the septum, *i.e.*, the rest of the body-cavity.

Excretory System.

The genital pores discovered by Kowalewsky, by which he observed the ova to pass to the exterior, are the external openings of a pair of nephridia. Each nephridium consists of a simple ciliated tube, whose cell-walls are filled with brown concretions. *The tube opens into the posterior chamber of the body-cavity* on the sides of the lateral mesenteries. The external openings are situated in the regions subtended by the anterior divisions of the body-cavity.

Circulatory System.

A closed system of vessels, containing nucleated red corpuscles, is present.

The main vessels are two in number.

The afferent vessel to the tentacles divides at the median dorsal region of the septum.

Each half passes into a vessel lying at the base of the tentacles. From this cæcal vessels pass into these. A second vessel lying outside the former is also by means of a valvular arrangement in communication with the same cæcal vessels in the tentacles. From the outside ring on either side passes a lateral vessel to the ventral side of the œsophagus, where, joining its fellow of the opposite side in the left anterior division of the body-cavity, it runs as the single efferent vessel to the hind end of the foot, giving off numerous cæcal vessels in its course.

Further, there is a sinus round the stomach. This arrangement will be understood when its development is described below.

The walls of all the vessels are contractile.

Generative System.

The animals are hermaphrodite. The ova and spermatozoa are formed from cells of the efferent blood-vessel, which runs in the left anterior chamber of the body-cavity. Round this vessel lies the so-called "fat body," which is composed of large cells developed on the wall of the cæcal prolongation of the blood-vessel. The ova and testis lie in this tissue on opposite sides of the main vascular trunk. Thus the nerve-cord and the generative cells are asymmetrically placed. They lie on the left side of the foot.

Development.

The following is a brief summary of the more important points:—

1. At the stage of four segmentation spheres, a division into two smaller clear and two larger opaque cells indicates the future ectoderm and endoderm.

2. The segmentation proceeds with considerable regularity, and results in a planula with half the cells smaller and less columnar than the other half.

3. Invagination of the larger cells almost obliterates the segmentation cavity, and a spherical gastrula with a blastopore is the final result of invagination. The gastrula becomes oval by the growth forwards of the ectoderm to form the præoral lobe, and the blastopore persists as the mouth.

The mesoblast is formed bilaterally from the endoderm on either side of the blastopore. From the time when two or three mesoblast cells are budded off on either side a cavity is present in each mass so formed. These cavities are the two halves of the body-cavity. I regard this

mode of origin of the body-cavity as a modification by simplification of the enterocœl type, as described by Kowalewsky, in Argiope.*

Quite recently Metschnikow† has described the early stages of Phoronis. His account is very different to that given above. In the first place, he has not detected the origin of at least the main part of the mesoblast from the endoderm, as I have described. Further, Metschnikow has figured a blastula with four mesoblast cells in the segmentation cavity. Though I have made numerous complete series of sections through all stages of the blastula, I never have found any cells in the segmentation cavity. I would offer the following explanation of Metschnikow's account.

When the invagination to form the gastrula begins, the hypoblast cells previously cylindrical become very irregular, and project pseudopodia-like into the segmentation cavity. The free ends of these cells in actual sections are frequently cut off from their origin, and may then be mistaken for free cells lying in the segmentation cavity. They, however, never contain the nuclei of the cells. I would suggest that Metschnikow, who studied the development of Phoronis by means of optical sections of glycerine preparations of the whole larva, has mistaken these projecting ends of the amœboid endoderm cells for mesoderm cells.

Rapid growth of the mesoblast "diverticulum" into the præoral lobe takes place in such a way that distinct somatic and splanchnic layers, applied to the ectoderm and endoderm respectively, are easily to be recognised.

The cells soon become contractile, and the whole præoral lobe almost immediately after its appearance becomes actively so. The muscle cells have all the histological character of Mesenchyme, using this term in the sense used by the brothers Hertwig.‡ Meanwhile the ectoderm becomes thickened in two regions—

1. In the præoral lobe.
2. In the form of a postoral ring round the mouth.

The former becomes the future nervous ganglion; the latter indicates the position of the line of future tentacles and the circum-œsophageal nerve-ring of the older animal.

The anus is formed by a slight invagination of ectoderm behind the postoral ciliated ring on the opposite side of the body to that on which the mouth is placed, and is from the first terminal. The four divisions of the alimentary canal are now apparent, *i.e.*, the hypoblast cells have taken on their characteristic form in the several regions of

* A. Kowalewsky, "Protocol of the First Session of the United Sections of Anatomy, Physiology, and Comparative Anatomy at the Meeting of Russian Naturalists in Kasan, 1873 (Russian)."

† "Z. f. Wiss. Zool.," Ht. IV, 1882.

‡ "Die Cœlom-theorie," Jena, 1881.

the alimentary tract. The cells of the first stomach, however, *though ciliated*, are much more amœboid than in the adult. Throughout larval life *intra-cellular* digestion goes on in this region. This mode of digestion ceases with the metamorphosis.

With the formation of the anus this end of the body gradually grows out. The papilla with the anus at its end enlarges, and finally forms the largest part of the full-grown larva. Tentacles appear in pairs as outgrowths along the lines of the postoral ciliated ring, new tentacles appearing dorsally.

The further development of mesoblast proceeds always in continuity with the first pair of lateral diverticula. The body-cavity of the hind end of the larva is formed independently in a paired mass of cells which grows out from the end of the first formed sacs, and remains separated from the latter by a septum.

Thus the *whole mesoblast of the animal arises as two endodermic sacs*, the walls of which form somatic and splanchnic layers.

Nephridia.

On either side of the body lies a ciliated canal with cellular walls. This canal is *not* formed of perforated cells.

Each canal opens to the exterior behind the septum on either side of the opening of the foot. The canal lies *outside* the somatic mesoblast.

Attached to its inner blind end are a number of cells of very peculiar form. Each cell has a nucleus and processes similar to those of ordinary mesoblast cells. By one of these the cell is attached to the end of the large canal. This process is larger than the free processes, and has a cylindrical form. By the canal formed inside the cylinder, small brown concretions seen in the cell itself pass into the large canal, and so to the exterior. These excretory cells, with their fine canals, increase in number with the growth of the larva. They float freely in the body-cavity in front of the septum.

The cells are similar to the perforated cells which form the internal ends of the nephridia described by Hatschek in Echiurus.*

At no time during the free swimming life of larva does the excretory canal system open into the body-cavity.

With regard to the development of the nephridia I have observed somatic mesoblast cells, at the time when the mesoblastic sacs of the trunk are forming, take the characteristic shape of excretory cells with cylindrical processes.

On the other hand, I have failed to discover the origin of the main ciliated canal.

* Berthold Hatschek, "Ueber Entwick. von Echiurus," Arbeit. a. d. Zool. Instit. Wien, vol. iii, 1880.

Dr. Hatschek believed that the whole organ was formed from the mesoblast cells mentioned above.

Vascular System.

The blood-vessels are all formed from the splanchnopleure.

The blood-corpuscles found in the vessels immediately after metamorphosis arise from mesoblast cells in front of the septum.

They form in masses which vary in number and position with the species, and lie free in the body-cavity held together by processes resulting from incomplete division. Each corpuscle has a nucleus, and with the growth of the larva the hæmoglobin colour gradually develops.

The vessels arise as splits in the splanchnopleure. The adult condition is reached partly by constrictions, partly by outgrowths from these. Thus we have at the close of larval life the blood-system in the following condition:—

1. Blood-corpuscles aggregated in two or more masses, lying free in the body-cavity of the præoral lobe, *i.e.*, in front of the septum.
2. A blood-vessel formed on the dorsal wall of the stomach, a marked structure in the larva.
3. The splanchnopleure sac, which in the region of the stomach forms a loose sac surrounding the gut.
4. Cæcal prolongations of this sac.
5. Cæcal prolongations into the rudiments of the adult tentacles.

Lophophore.

The larval tentacles are produced in pairs always towards the dorsal line, so that the most dorsal are the youngest. This is also the case in the adult Phoronis.

But the first rudiments of the adult set appear laterally, and new pairs are added both ventrally and dorsally to this pair, so that the oldest adult tentacles are not the most ventrally situated.

Full-formed Larva and Metamorphosis.

Finally we get the full grown free swimming larva, whose chief organs and their relative positions I shall briefly recapitulate.

The mouth and anus are at opposite ends of the ciliated body. The mouth is overhung by a large præoral lobe, whose margin is slightly thickened, and bears longer cilia than on the rest of the surface. This margin corresponds to the velum (præoral ring) of other larva.

I reserve the discussion of Kleinenberg's paper* on the origin of the

* N. Kleinenberg, "Sull' Origine del Sistema Nervoso Centrale degli Annelidi." Reale Acad. d. Lincei, 1881.

nervous system, for my fuller paper. The bearing of the facts of Phoronis development on the question would involve matter of a too speculative character. Suffice it to say, that if the nerve-ring of Phoronis represents the nerve-ring of Cœlenterate ancestors, the præoral lobe must be regarded as a development of an anterior region of the sub-umbrella, while the anus has been formed in the region of the umbrella.

The nervous elements of the ectoderm of the præoral lobe in all species, are concentrated into a ganglion (Scheitelplatte). In some species a large number of nerve fibres pass forwards from it to a sense organ. In one species four eye-spots are present. Behind the mouth an even number of tentacles form a postoral circlet. Behind these, and corresponding in number, lie rudiments of the adult tentacles. Along a line immediately in front of the larval circle, the ectoderm cells have become vacuolated. This change extends to a breadth of only three or four cells. Along a line at the base of the rudiments of the adult tentacles, the nervous prolongations of the ectoderm have formed a definite ring.

Round the anus a ring of very columnar ectoderm bearing strong cilia forms the chief organ of larval locomotion. The mouth opens into an œsophagus, which leads into a stomach. The stomach at its anterior end is produced into one or two ventral recesses.

In the vacuolated walls of these structures brown concretions are present.

The septum is attached in a circle along the line of the nerve-ring, and free communication exists between the body-cavity in front of the septum and the split in the splanchnopleure, which will form the blood sinus and vessels of the adult.

The condition of the rest of the vascular system we have already described in an old larva. The muscular arrangement in the invaginated foot is already similar to that in the adult.

The ventral mesentery still exists along the whole ventral surface from septum to anus. The pair of nephridia lie on either side of the body, their numerous excretory cells floating freely in the body-cavity in front of the septum. The external openings are placed one on either side of the opening of the foot.

The animal now swims to the bottom, and after swimming round and round many times on its own axis, and meanwhile undergoing violent contractions, suddenly begins to evaginate the foot. In fifteen to twenty minutes, a healthy individual will have become in all essential points like the adult.

During this time the following events take place:—

i. The whole præoral lobe with ganglion and sense organs pass into the stomach by the œsophagus. The rupture takes place along the line of vacuolated ectoderm mentioned above.

ii. The larval tentacles follow the præoral lobe.

iii. The blood-corpuscles pass inside the splanchnopleure sac by the opening described above, and break up in the sinus. From this they pass by contractions of the sac into the cæcal vessels and into the vessel which already exists in the dorsal side of the stomach.

iv. The larval excretory cells of the nephridia break off from the large canal and float freely into the body-cavity in front of the septum. They pass with the blood-corpuscles into the vessels. The *large canals remain as the paired nephridia of the adult.* The external openings by the changes undergone during the evagination have already almost their adult position.

v. The body-wall of the anal cone (at this stage) becomes folded, so as to present the appearance of columnar epithelium. By this process the invagination of the whole anal cone is rendered possible. The original anus is now half-way up the course of the ascending limit of the alimentary tract inside the foot, and the adult position of the nerve-ring is thus brought about.

The ventral mesentery extends along the outer curve of the alimentary tract along its whole extent, attaching the foot to the body-wall. At the end of the body it is seen in end view, apparently as a linear band, presenting a similar appearance to the funiculus of a polyzoon.

The ectoderm, from what has been said, must now re-attach itself by a secondary growth to the endoderm, along the lines where the præoral lobe broke off.

In the stomach the disintegrated cells of the tentacles and the præoral lobe with its ganglion and sense organs are now digested, not, however, by intercellular method, but, as in the adult, in the canal itself.

General Conclusions.

The life history of Phoronis, the chief points in which have been briefly mentioned, seems to offer a solution of many morphological problems.

These are of two kinds.

On the one hand we have those more general questions which concern the origin of various organs and systems of organs.

On the other those special problems which are concerned in solving the body plan of the different animal forms.

On the Origin of Organs and Organ Systems.

The condition of nervous concentrations in the ectoderm in Phoronis, both larval and adult, shows us how apparently new parts of the nervous system arise.

In Phoronis the præoral ring, corresponding to the velum of a

Trochosphære, is from the earliest stages reduced relatively to the postoral.

This latter, appearing in the gastrula stage, persists throughout life as a circumœsophageal ring. No anterior dorsal sensory part of the central nervous system exists in the adult.

The ganglion of the præoral lobe which in Chætopoda and Mollusca, &c., persists as the anterior sensory lobe of the brain, disappears with the change from a free to a fixed life.

The ganglion sense organs and velum of the præoral lobe are eaten during the metamorphosis.

The pair of sense organs are connected with the postoral nerve-ring.

In Capitellidæ, Dr. Eisig has been kind enough to inform me, the nerves from the ciliated pits are connected not with the anterior lobes of the brain, but with the posterior part from which the circumœsophageal commissures are given off.

Body-Cavity.

The whole body-cavity in the præoral lobe and in the trunk is an enterocœl. The closed vascular system is developed from the spanchnopleure. The intracellular excretory canals arise in somatic mesoblast cells. The existence of two divisions of the excretory system, viz.,

i. The intracellular closed canals;

ii. Large intercellular canals;

ceases with the metamorphosis. In Phoronis the atrophy of the intracellular system is coincident with the development of the vascular system.

If the intracellular excretory system of larval Phoronis is homologous with the similar excretory system in Platyelminthes, there is a presumption that the cavities in which the cells lie are homologous, that in fact Platyelminthes are degenerate enterocœles.

On the Relation of Phoronis to other Groups.

The most striking result of my researches on Phoronis is to give an explanation of the relation of Brachiopoda and Polyzoa to other animals. The identity of the Phoronis larva up to the formation of the nephridia, and before the outgrowth of the anal region, with the Trochosphære type of Hatschek is complete.

In Phoronis the body-cavity is an enterocœl. The distinction attempted to be drawn by the Hertwigs* between the histological characters of mesenchyme and mesoderm utterly breaks down in Phoronis.

I regard it, therefore, as probable that the other Trochosphæres are enterocœles.

* O. and R. Hertwig, *loc. cit.*

The larvæ of Brachiopoda and Polyzoa I regard as modified from the Trochosphære by the earlier attainment of the relation of the ventral surface which in Phoronis is only accomplished during the metamorphosis.

Phoronis and Brachiopoda.

The conception of the body plan of Brachiopoda arising in this way involves an entirely new view of the homologies of the body surfaces. The following are the chief points which seem to me to determine these :—

1. The præoral lobe of the larva of Phoronis, and the so-called "segment" which bears the eye-spots in certain larval Brachiopoda* persist in part at least as the epistome of the adult.

2. There is a postoral nerve-ring in all the Brachiopoda I have examined) situated as in Phoronis in the ectoderm.

3. In both the body-cavity of the præoral lobe is separated from that of the rest of the body by a septum.

4. The "segments" of Brachiopoda are represented in Phoronis by the three divisions of the larva.

1. Præoral lobe as far back as the septum.
2. The rest of the body to the anal ring.
3. The invaginated foot.

An evagination similar to that in Phoronis of the third "segment" takes place in Brachiopoda when the larva fixes itself (Morse, Terebratulina.)

5. The tentacles arise from the line of the nerve-ring and are in the form of a horse-shoe, the outer curve of which is ventral. In the middle of the inner curve there is a break in the continuity of the tentacles. This interval is in the median dorsal line. On either side lies one of the youngest pair of tentacles.

6. The rectum when present lies in the posterior of the three main divisions of the body-cavity formed by the ventral and two lateral mesenteries (vide diagram B). The nephridia open to the interior in the posterior, to the exterior in the region of the anterior chambers of the body-cavity.

7. The same four divisions of the intestine are formed in both Phoronis and Brachiopoda.

Finally, I would point out that the so-called *segments of Brachiopoda are at right angles to the ordinary Chætopod segments.* This is easily seen to be the case by reference to the diagram, where AB represents the axis perpendicular to which ordinary segmentation takes place, CD that perpendicular to which Brachiopoda have been supposed to be segmented.

* Kowalewsky, *loc. cit.*

Brachiopoda are thus fixed by their ventral surface.

The dorsal surface is indicated by the epistome, and the line between mouth and anus (when present).

Both valves of the shell are ventral.

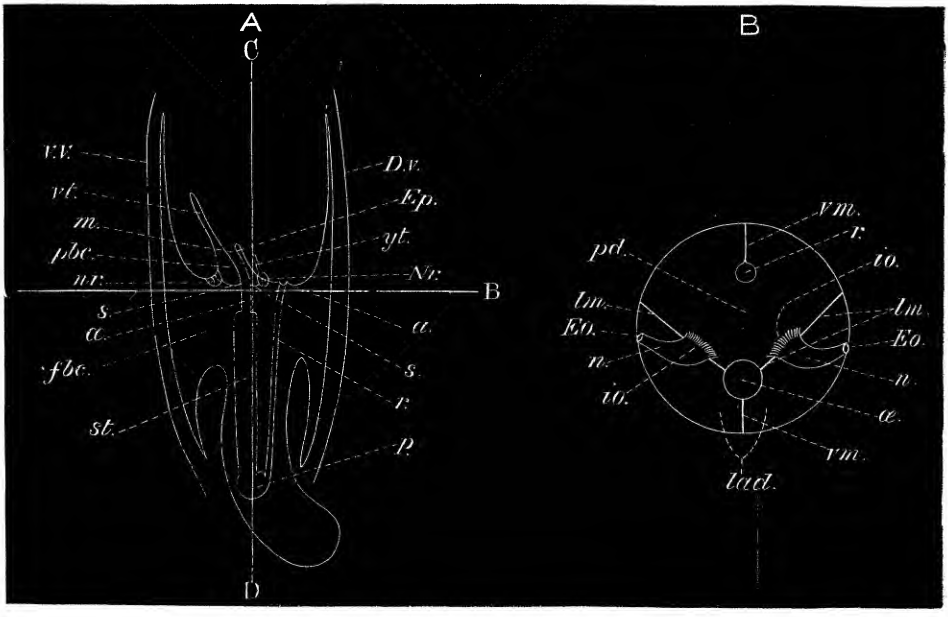
Phoronis and Polyzoa.

With regard to the Polyzoa, the evidence owing to the simplification which has taken place in their structure is not obtainable in the same quantity. I regard it, however, as probable that the epistome of Endoproct and Hippocrepian Polyzoa and the "foot" (Ray Lankester) in Rhabdopleura represent the præoral lobe.

The dorsal surface in Polyzoa is indicated as in Phoronis by the line between mouth and anus. If Phoronis, Brachiopoda, and Polyzoa have had segmented ancestors no trace of such remains in their ontogeny.

The discussion of the various views at present held on the Polyzoa and Brachiopoda must be deferred to my fuller paper.

So far as the facts of development and structure of Sipunculus and Phascolosoma are known, I see nothing to show that these forms are not referable to the same type of body structure as Phoronis, Brachiopoda, and Polyzoa. On the other hand, it seems quite possible that they may be further stages in degeneration from forms like Echiurus, which, after the researches of Hatschek, seem to be degenerated Chætopoda.

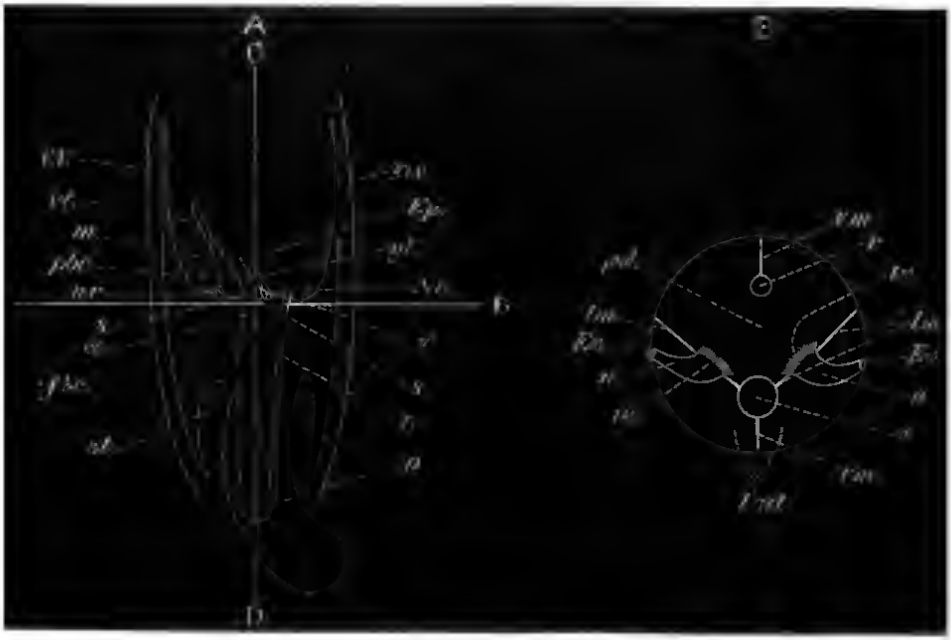


Two diagrams to illustrate the body plan of Phoronis, Brachiopoda, and Polyzoa.

A. Longitudinal vertical section through the adult animal.
B. Longitudinal horizontal section through the adult animal.

E.p. Præoral lobe or epistome.
m. Mouth.
a. Anus.
œ. Œsophagus.
s.t. First stomach.
p. Second stomach.
r. Intestine.
v.t. Right tentacle of ventral pair.
y.t. Right tentacle of dorsal pair.
p.b.c. Body-cavity of head.
f.b.c. Body-cavity of foot.
N.r. Postoral nerve-ring.
v.m. Ventral mesentery.
l.m. Lateral mesentery.
n. Nephridium.
E.o. External opening of nephridium.
i.o. Internal opening of nephridium.
p.d. Posterior chamber of body-cavity.
l.a.d. Lateral anterior divisions of body-cavity.

V.V. and D.V. Valves of Brachiopod shell.
A.B. Represents axis perpendicular to which ordinary segmentation takes place.
C.D. Represents axis perpendicular to which Brachiopoda have been supposed to be segmented.



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